Breeding failure and nestling body mass as a function of age of breeding females in the endangered Carnaby's Cockatoo, *Calyptorhynchus latirostris*

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ABSTRACT

The ecology of a population of the endangered Carnaby's Cockatoo, *Calyptorhynchus latirostris*, was studied from 1969 to 2015, with breeding data collected for 28 of those years. Data were available on the known breeding failure rates of females of known age (banded as nestlings in the study area) and females of unknown age (banded as adults), and on the condition of their nestlings, as assessed by the nestlings' body mass and age. Females in their first two breeding years had failure rates four times that of older and more experienced females. Younger females (4 to 6 years old) were more likely to nest up to three weeks later than older females (7 to 27 years old), and the oldest females in the study area were more likely to nest three weeks later than those at least 10 to 19 years old. There was a trend for oldest females to produce lighter nestlings than young females. Despite the length of the study, few data are available on longevity in the species, other than one known age female breeding in her 27th year, and one female of unknown age breeding when she was at least 30 years old. Nestling body mass is a useful indicator of population health, and more breeding populations of Carnaby's Cockatoo should be monitored to assess the likelihood of their persisting in the long-term.

Key words: age-related breeding failure; nestling body mass; relationship between female age and nestling body mass; longevity

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Introduction

Carnaby's Cockatoo, *Calyptorhynchus latirostris*, is endemic to south-western Australia. The species has undergone an extensive decline in range and abundance since south-western Australia was settled by Europeans early in the 19th Century. The settlers rapidly changed the landscape by clearing native vegetation to establish broadscale agriculture and urban settlements (Saunders 1990) (Figure 1). The resulting loss of foraging and breeding habitat is the main cause of the species' decline. Carnaby's Cockatoo is listed as endangered under the Australian Federal Government's *Environment Protection and Biodiversity Conservation Act* 1999, listed as "Fauna that is rare or likely to become extinct" in Schedule 1 of the Western Australian *Wildlife Conservation Specially Protected Fauna Notice 2015* under the *Wildlife Conservation Act 1950*, and listed as endangered under IUCN Red List category and criteria (IUCN 2014). IUCN has recently introduced the nomenclature *Zanda latirostris*, but we use *Calyptorhynchus latirostris* as specified in Western Australian Government regulations. The species is the subject of a recovery plan which operated from 2002 to 2012 (Cale 2003), and which has been revised recently (Department of Environment and Conservation 2012).

A breeding population of Carnaby's Cockatoo at Coomallo Creek in the northern wheatbelt of Western Australia (Figure 1) has been studied since 1969, and is still subject to research and monitoring (Saunders *et al.* 2014b and references therein). In this paper we report on breeding failure rates of individually marked females in this population, including females of known age that were banded/ringed as nestlings in the area. Saunders (1986) and Saunders *et al.* (2015) established that body mass of nestlings is a function of nestling age. In this paper we examine whether nestling body mass is also a function of the age of the female parent. We hypothesise that young females, and by implication, less experienced female parents, produce nestlings that are lighter than those produced by older, and presumably more experienced females, and old females, as they become less efficient at

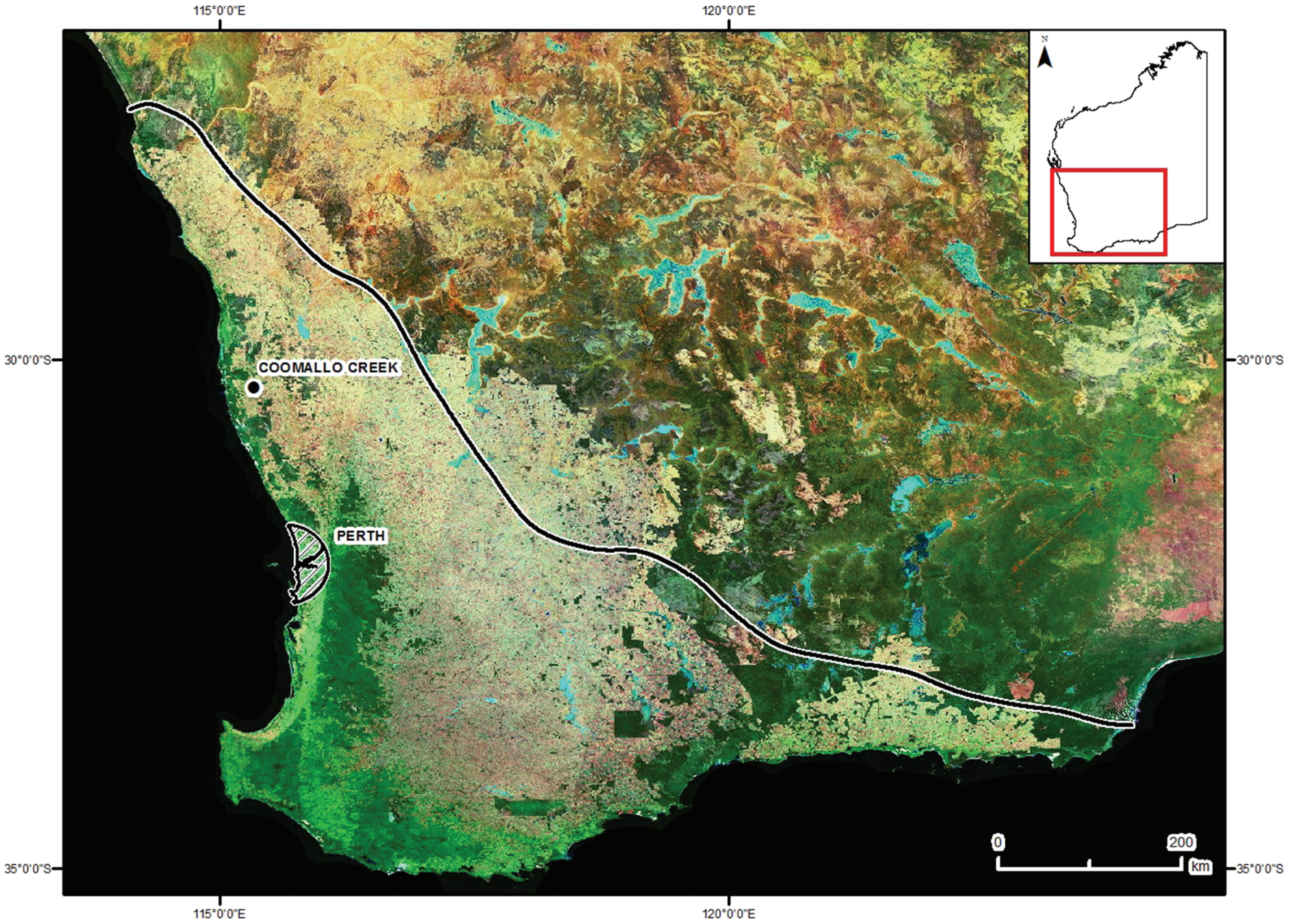

Figure 1. Location of Coomallo Creek study area and distribution of Carnaby's Cockatoo (between the coast and the black line). The extensive clearing of native vegetation (shown in pale yellow) throughout the range of Carnaby's Cockatoo is clearly illustrated.

provisioning nestlings, also produce lighter nestlings. We then discuss the conservation implications of our findings.

Methods

Carnaby's Cockatoo

Carnaby's Cockatoo forms long-lasting pair bonds, usually for the life of one of the partners (Saunders 1982). Data suggest that breeding adults attempt to breed every year in the same area. Females use the same hollow they used the previous season, provided they were successful in fledging young the previous year, and the hollow is unoccupied when they return to the area to breed. If they move to a different hollow it will usually be close to the previous hollow, although they may move up to several kilometres in the same area of woodland (Saunders 1982). One to two eggs are laid, sometime between June and December. Two is the most common clutch size. Between 1969 and 2015, 79% of eggs were laid in August and September (Saunders and Dawson *unpublished data*). The second nestling usually dies within 48 hours of hatching, although the second nestling may also be raised successfully, usually by older females (Saunders 1982; Saunders *et al.* 2014b). Breeding females are dependent on their male partners for food during incubation which lasts 28-29 days, and the first few weeks of the nestling period which lasts 70-77 days. Both parents feed the nestling(s) (Saunders 1982; Saunders *et al.* 2014b,c). Most females commence breeding in their 4th year, but females have been recorded attempting to breed in their 3rd year (Saunders and Ingram 1998; Dawson *et al.* 2013; Saunders and Dawson *personal observations*).

One breeding population of Carnaby's Cockatoo at Coomallo Creek (Figure 1) has been studied from 1969 until the present (Saunders *et al.* 2014c), with the population being monitored for 21 years between 1969 and 1996, and seven years between 2009 and 2015. From 1969 to 1994, breeding females were trapped in their nest hollows, and individually marked with a stainless steel leg band (Figure 2). Up to 1976 they were also marked with a stainless steel patagial tag (Saunders 1988). Sixteen females were also banded with two colour bands (Figure 2). No adult females have been banded at Coomallo Creek since 1994.

During every visit to the breeding area, attempts were made to sight all breeding females when flushed from the hollow to check for patagial tags and leg bands, identify the females by photographing the bands (Figure 2), and

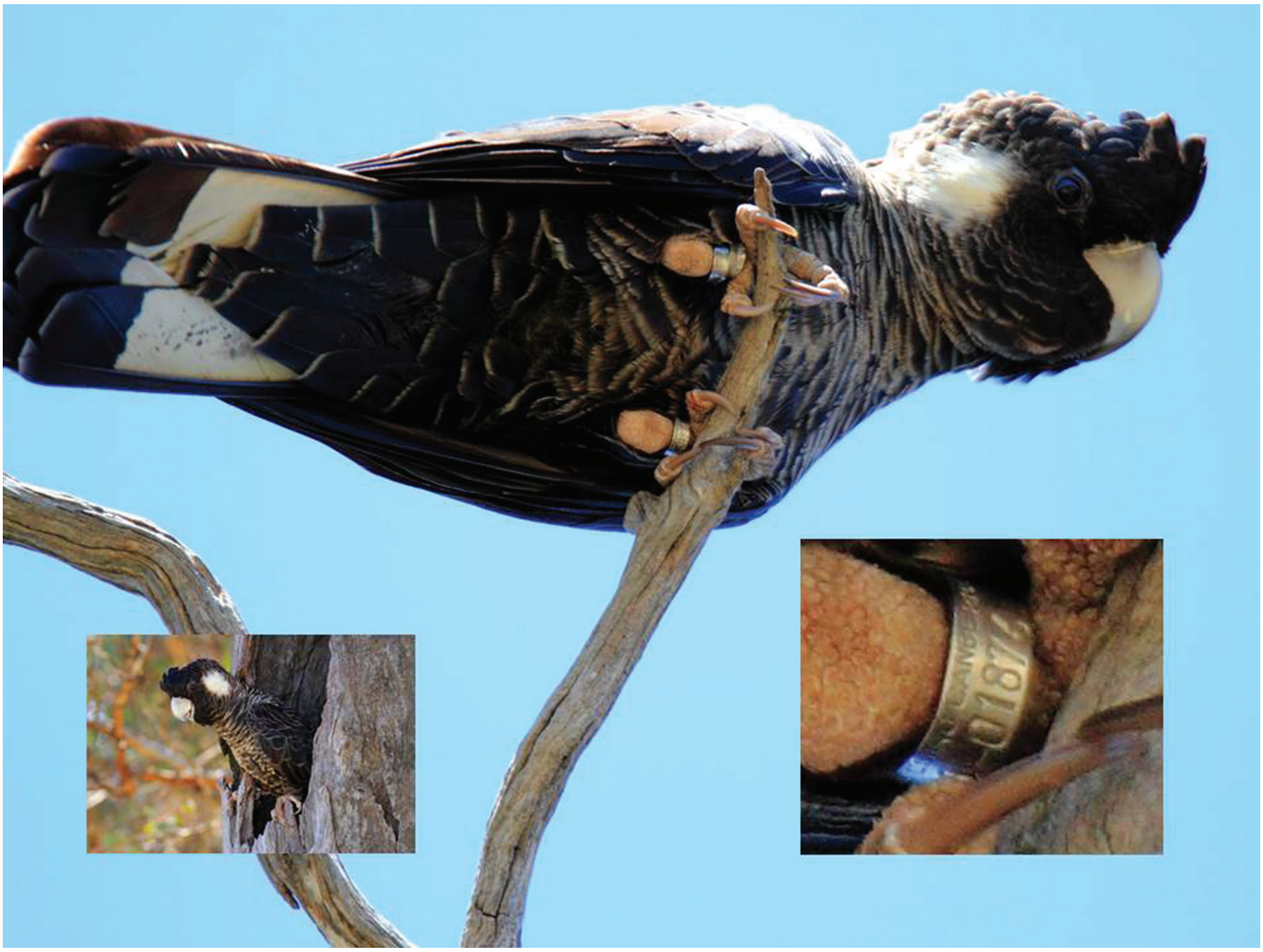

Figure 2. Female Carnaby's Cockatoo, band number 210-01876, showing the numbered band on the right leg (with the inset showing the last five numbers), and the two colour bands on the left leg. When new the colour bands were orange over yellow, but over the 26 years they have been on the bird the paint has worn off. The other inset shows the female sitting in the entrance to a nesting hollow. This female was last seen at Coomallo Creek in 2014 when she was at least 30 years old.

establish the results of their breeding attempts. In the period up to 1996 it was difficult to identify marked individuals without recapturing them; a time consuming and not very successful method. With the technological advances in digital photography, since monitoring resumed at Coomallo Creek in 2009, it has been possible to photograph the legs of most of the breeding females and identify any that were banded (Saunders *et al.* 2011a).

The number of visits each breeding season varied; in most years restricted to two visits (early September and early November) following the monitoring protocol of Saunders and Ingram (1987). From 2009, the area was also visited in January. In some cases the results of breeding could be established during the second or final visit for the breeding season; that is, the nesting attempt had failed or the nestling had fledged. In other cases, for example where nestlings were still present during the second or final visit for the season, the results were not known. Failure was more common during incubation, but failure may happen during the nestling period. Because the results of all nesting attempts may have not been established every season, rather than potential breeding success being used in the analyses, known failure rates have been used. These are minimum estimates of failure rates.

Aging breeding females

Those breeding females that were banded at Coomallo Creek as nestlings were classed as "known age females". Those that were banded as adults were classed as "unknown age females", and were regarded as at least 4 years old when banded. Their age in subsequent years was assigned on the basis of them being at least 4 when banded. That is, a female banded as a breeding adult in 1970 was regarded as 4+ then, and 7+ if recorded breeding in 1973.

Aging nestlings and extrapolating laying dates

Over 27 years at Coomallo Creek, from 1970 to 2015, 1112 nestlings were measured a total of 2183 times; the majority only once, with one individual measured 10 times. Of these nestlings there were 32 that were offspring of known age females (generating 41 observations) and 316 nestlings of unknown age female parents with a total of 1046 sets of measurements. Measurements taken were the length of the folded left wing (mm) and body mass (g) (Figure 3). Any nestling over 21 days old was individually marked with a stainless steel leg band from the Australian Bird and Bat Banding Scheme. Each nestling was aged in one of two ways. If the nestling was first seen on the day it hatched its age was accurately known. If not, it was aged by comparison with a table of the growth of folded left wing of known aged nestlings following the method outlined by Saunders (1986) and Saunders *et al.* (2015). As there was no difference in body sizes between the sexes (Saunders 1974), this aging technique was applied to nestlings of both sexes. Laying dates were extrapolated from the estimated age of the nestling and an incubation period of 29 days (Saunders 1982).

Distances between nest hollows used by individual females

Coordinates of every known nest hollow in the study area were recorded on a global positioning system, and plotted on a Google Earth satellite image of the study area. Distances between nest hollows used by individual females were established using the "Show the distance between waypoints" function on OziExplorer (D&L Software Pty Ltd).

Analyses

Nestling body mass was regressed against nestling age and the age of the female parent using a generalized additive mixed model (GAMM) (Wood 2011). Initial modelling was undertaken using the smaller data set (41 observations) of nestlings of known age female parents and separately using the 1046 observations of nestlings of unknown age female parents. Nestling identity was used as a random factor to account for instances where multiple observations were made on the same nestling. The adequacy of the generalized additive smoothing was checked by increasing the smoothing parameter from the default value of nine to either 18 or the maximum possible number for the known age female data set. In all cases there was no evidence that the selected smoothing was constrained by the use of the default smoothing parameter. Preliminary modelling suggested that the response variable, nestling body mass should be transformed using natural logarithms which removed any evidence of heterogeneity in the variance of the residuals as a function of the fitted values. For each model, fitted standard regression diagnostics (Cook and Weisberg 1982) were inspected for heterogeneity in the residuals, pattern in the residuals plotted against the fitted values and for evidence of a departure from a normal distribution.

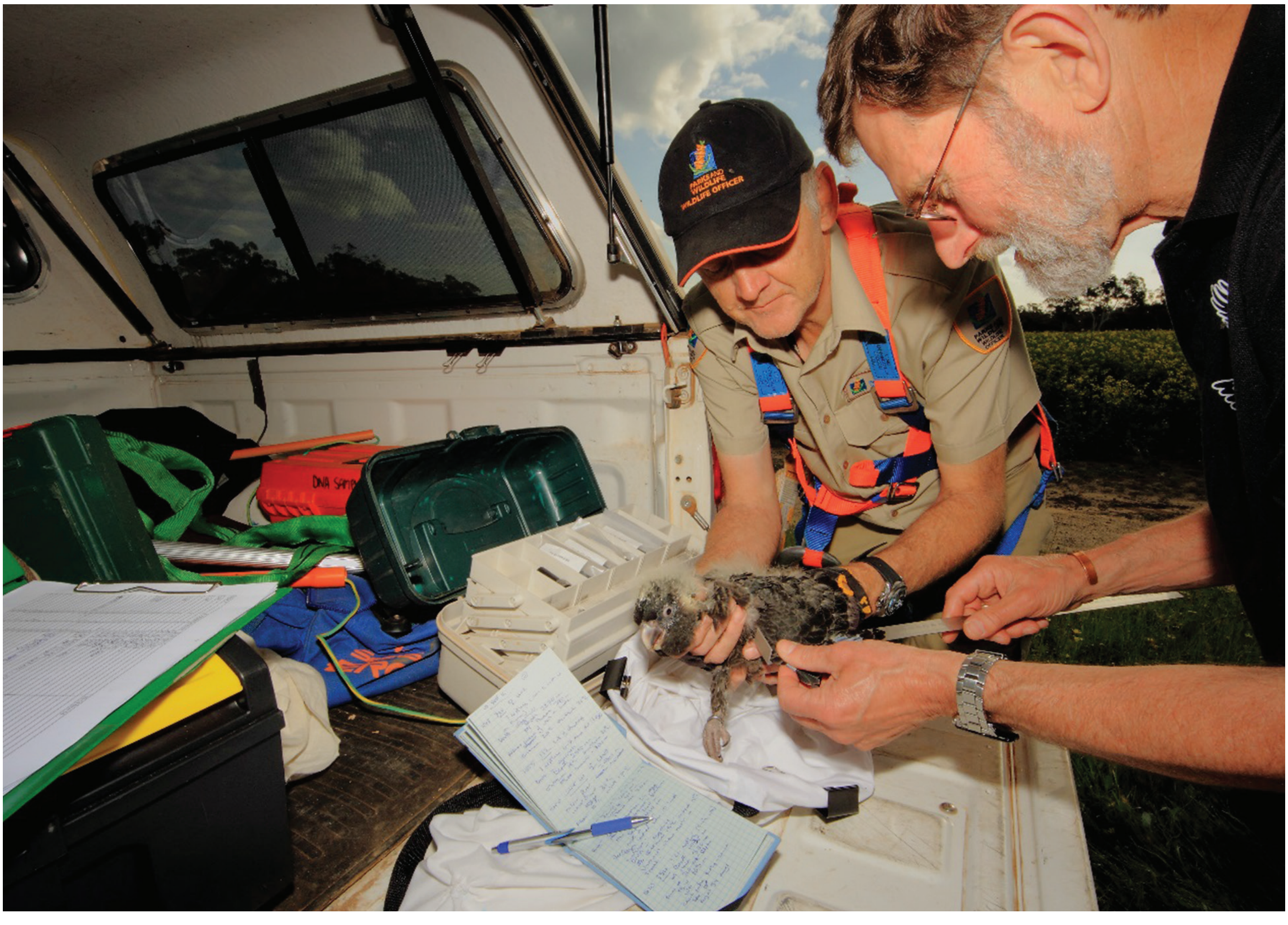

Figure 3. Rick Dawson (left) and Denis Saunders measuring the folded left wing of a Carnaby's Cockatoo nestling (Photograph Matt Swan).

All analyses were conducted in R version 3.2.2. (R Core Team 2015) and followed recommended procedures for generalized additive mixed models (GAMM) (Wood. 2011) and data collation and manipulation (Sarkar 2008; Venables 2013).

Results

Breeding data from females of known and unknown age

The breeding failure rates of females of known age in their 3rd and 4th years, and 5th to 27th years, and females of unknown age 4+ and 5+, 6+ to 10+ and 11+ and older are shown in Table 1. Two females laid eggs in their 3rd year, but both failed to hatch the eggs. The breeding failure rate of females breeding in their 3rd and 4th years (45.5%) was over four times that of known age females breeding in their 5th year and older, but not statistically significant (p = 0.08 Fisher's exact test), and over three times that of unknown age females from 4+ to 30+ (Table 1). The failure rate of 14 breeding attempts by the three older unknown age females at least 19 to 30 was 14.2%, similar to the 13.4% of all breeding attempts by females of unknown age. For the 12 breeding attempts by three females breeding from 25 or 25+ and over, the failure rate was 8.3%.

The average distance between the hollow from which a female fledged and the hollow in which she was first recorded breeding was 2.41 km (n = 23). These distances ranged from 0km (nested in the hollow from which it fledged) to 8.18 km (from nearly one end of the study area to the other). The average distance between hollows used successively by 106 females was 0.28 km (n = 124), ranging from 0 to 1.95 km. 46.0% nested in the same hollow the following season and 60.5% nested in the same hollow or within 100 m of the previous hollow (Figure 4).

The breeding season of 2014 was when fledglings banded in 2009 would be expected to commence breeding in their 4th year. Two known age females commenced breeding in 2014; one was in her 3rd year and the other was in her 4th year; both were unsuccessful. There were 101 breeding attempts recorded in the study area in 2014, and the population of breeding females that year consisted of a minimum of 2.0% of first breeders. In 2015 3.0% of breeding females were in their 3rd or 4th year. We do not know the age of the males with which they were mated.

Relationship between age of breeding females and body mass of their nestlings

The relationship between the observed nestling body mass and nestling age is shown in Figure 5, and between nestling body mass and the age of the female parent in Figure 6. It is clear from Figure 5 that the data for nestlings of known age females lie well inside the range of observations of nestlings of unknown age females. The important message from Figure 6 is the variation of nestling body mass observed of nestlings of females of unknown age in the range 4+ to 7+ years; there are two important sources of this variation, the first is the differences in nestling body mass as a function of the age of the nestling when it was measured, and secondly for females of unknown age each age class contains an unknown range of ages from the nominated age to old birds.

Forty-one sets of measurements for nestlings of 15 females of known age from a total of 17 seasons were available for analysis. Of these 41 measurements, 26 are a single measurement of a nestling and the other 15 are measurements from four nestlings. 78% of the data were obtained from nestlings of females in their 3rd to 8th years, and 22% were obtained from nestlings of females in their 10th to 27th years. Nestlings of a total of 130 females were monitored; the majority of unknown age females (114 of 130) whose offspring were monitored for one to three breeding seasons. Only three females contributed nestlings that were monitored for eight to 11 breeding seasons. A total of 316 nestlings were monitored; of 1046 measurements available for analysis, 13.8% represent single measurements on 144 nestlings, and the remainder were

Table 1. Breeding failure rate of females of known and unknown age.

Females of known age	3-4	5-27		Total
# known failures	5	3		8
Total individuals breeding	11	27		38
% failures	45.5	11.1		21.1
Females of unknown age	**4+-5+**	**6+-10+**	**11+ -**	
# known failures	21	16	5	42
Total individuals breeding	172	101	41	314
% failures	12.2	15.8	12.2	13.4

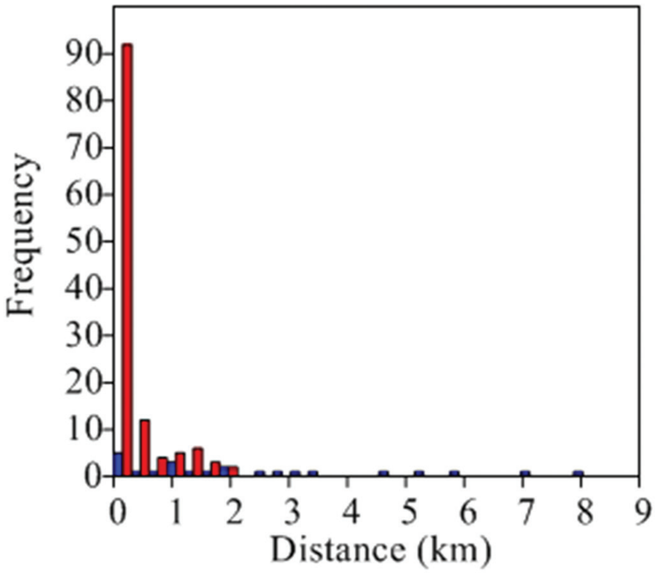

Figure 4. Distances between the hollows from which the females fledged and the first hollow they were recorded breeding in are shown in blue, and distances between successive hollows used by known age females in their 5th year and older and those of females of known age at least five and older are shown in red.

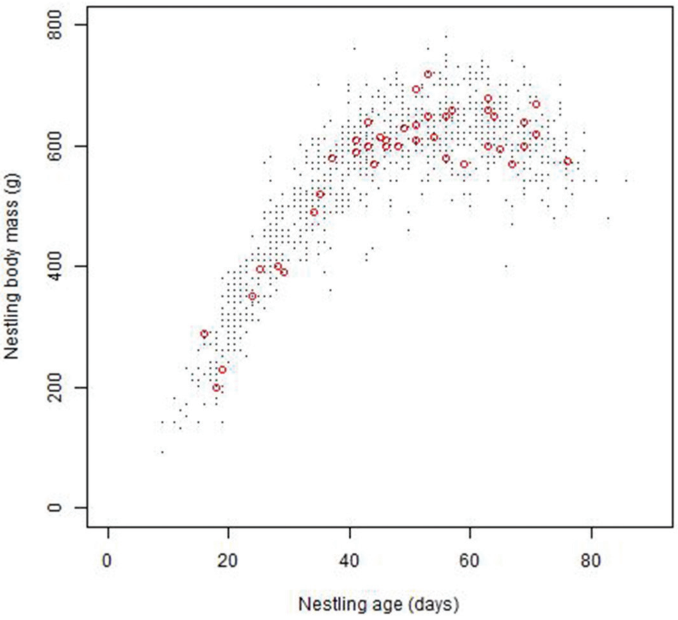

Figure 5. Observed body mass of nestlings of known age females (red circles) and unknown age females (black dots) as a function of nestling age.

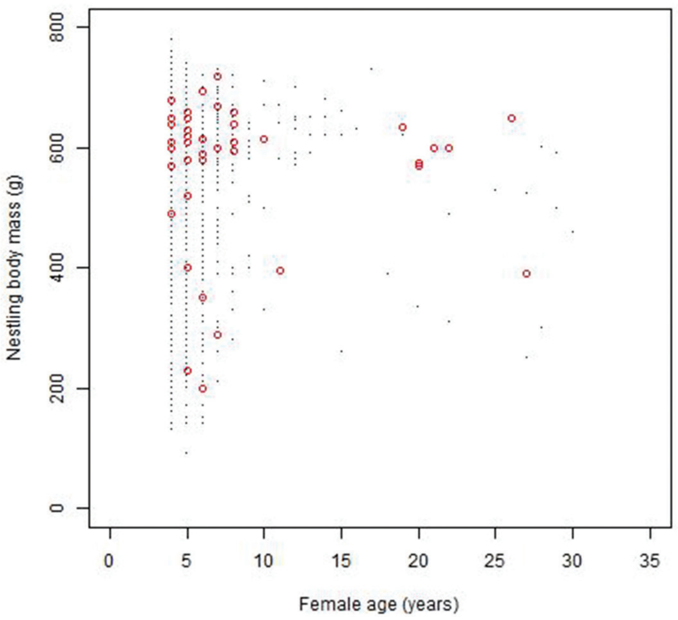

Figure 6. Observed body mass of nestlings of known age females (red circles) and unknown age females (black dots) as a function of female's age.

from 172 nestlings, with 63.6% coming from nestlings that were measured six or more (maximum 10) times. Of the data from nestlings of unknown age females the majority were nestlings from females that were aged as 4+ to 8+ years (94.9%), and only 3.9% were from nestlings of females that were aged 10+ 30+ years (Figure 6).

The two GAMM fitted to the log transformed nestling body mass data suggested that the response to female age was a linear first order polynomial function that was not significant ($p = 0.98$) for the data from known age females and significant ($p = 0.011$) for the unknown age female data set. In both cases the probability of the smoothing function for nestling age was substantially less than 0.001.

The components of the two models (for nestlings of known age females and nestlings of unknown age females) are shown on Figures 7 and 8. In both models it is clear that nestling age has a strong effect on nestling body mass, but the age of the female parent does not have an effect on the nestling body mass (Figure 7B). However, the model for the unknown age female data does indicate a trend that is consistent with the hypothesis that old females may produce nestlings that are lighter than those of young females (Figure 8B). The magnitude of the decline in nestling body mass for each increase of one year in female age is 0.991 (95% confidence interval is 0.985 to 0.998) (Figure 9).

Timing of egg-laying by individuals

The dates of the first egg laid by 15 females of known age and 99 females of unknown age were extrapolated from the estimated age of their nestlings following the method of Saunders et al. (2015). Laying dates were available for two to four breeding seasons for nine females of known age (3 with 2; 4 with 3; and 2 with 4 breeding seasons) and two to ten breeding seasons for 88 females of unknown age (50 with 2; 20 with 3; 9 with 4; 5 with 5; 1 with 7; 2 with 8; and 1 with 10 breeding seasons). As egg-laying may commence any time from the first week in June to December (data from breeding seasons 1969 – 2016), depending on autumn rainfall (Saunders et al. 2013), the timing of egg-laying by individuals was calculated in relation to Week 1 each season; Week 1 being the week in which egg-laying commenced that season. 40% of eggs from successive seasons were laid by known age females either in the same week as the previous season or plus or minus one week and 46% by unknown age females over the same time span (Table 2). Changes between successive seasons ranged from 10 weeks after, to 12 weeks before the previous season (Table 2). The majority of both known age (53%) and unknown age females (57%) laid eggs the following season within two weeks before or after the week they laid previous season. For example, female 210-01694 laid in week 4 when she was 19, week 2 at 20, week 4 at 21 and week 5 at 22. She was not recorded breeding in the study area from the time she was banded as a nestling until she was seen aged 19. This female was one of the birds that moved into the study area after extensive areas of breeding habitat to the south of the study area were burnt in a wildfire in late December 2009 (Saunders et al. 2014b). Female 210-00450 laid in week 4 when she was at least 4, week 4 at 5+, week 5 at 6+, week 2 at 11+, week 3 at 12+, week 3 at 13+, week 8 at 14+, week 6 at 15+, week 8 at 18+, and week 4 at 19+.

Timing of egg-laying in relation to age of females

The median start of egg-laying for known age females 4 to 6 years old ($n = 16$) was the 7th week after egg-laying

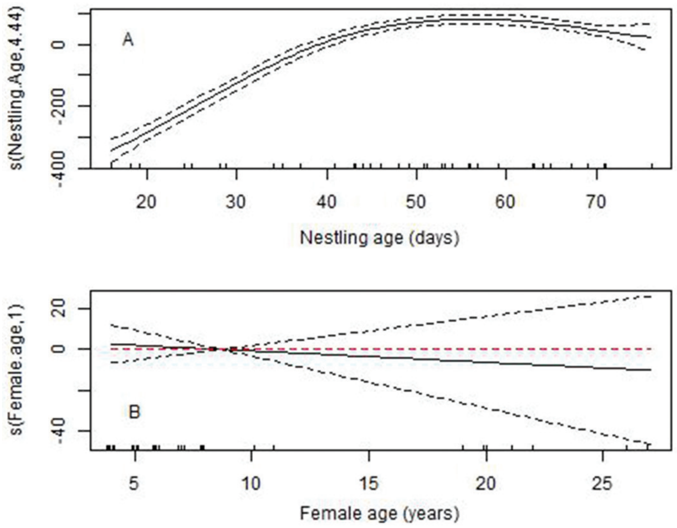

Figure 7. Components of the GAMM model fitted to all observations per nestling from nestlings of known age females. (A) shows the fitted effect of nestling age on log transformed nestling body mass, and (B) the fitted effect of female age on log transformed nestling body mass. The solid line represents the GAMM fitted values, the grey broken lines the upper and lower 95% confidence intervals and the red dashed line the line of no effect due to female age. The description of the ordinate axis gives the smoothed predictor and the effective degrees of freedom of the applied smoother. Note the different ordinate scales used in (A) and (B). The internal ticks along the X-axis indicate the distribution of data for nestling ages (A) and female ages (B).

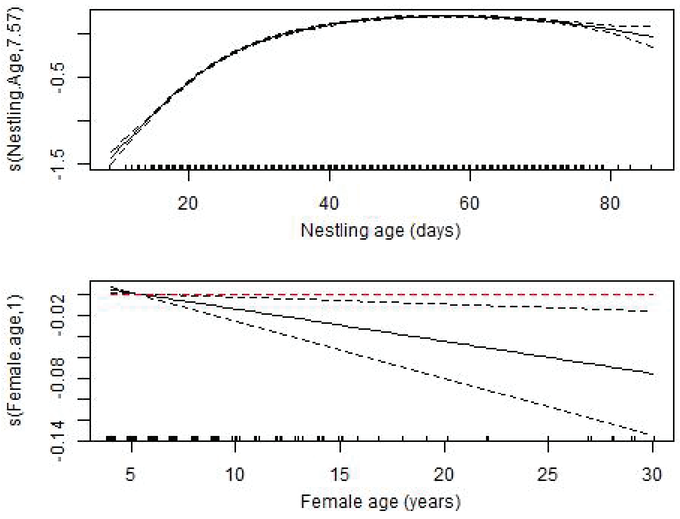

Figure 8. Components of the GAMM model fitted to all observations from nestlings of unknown age females. (A) shows the fitted effect of nestling age on log transformed nestling body mass, and (B) the fitted effect of female age on log transformed nestling body mass. The solid line represents the GAMM fitted values on a log scale, the grey broken lines the upper and lower 95% confidence intervals and the red dashed line the line of no effect due to female age. The description of the ordinate axis gives the smoothed predictor and the effective degrees of freedom of the applied smoother. Note the different ordinate scales used in (A) and (B). The internal ticks along the X-axis indicate the distribution of data for nestling ages (A) and female ages (B).

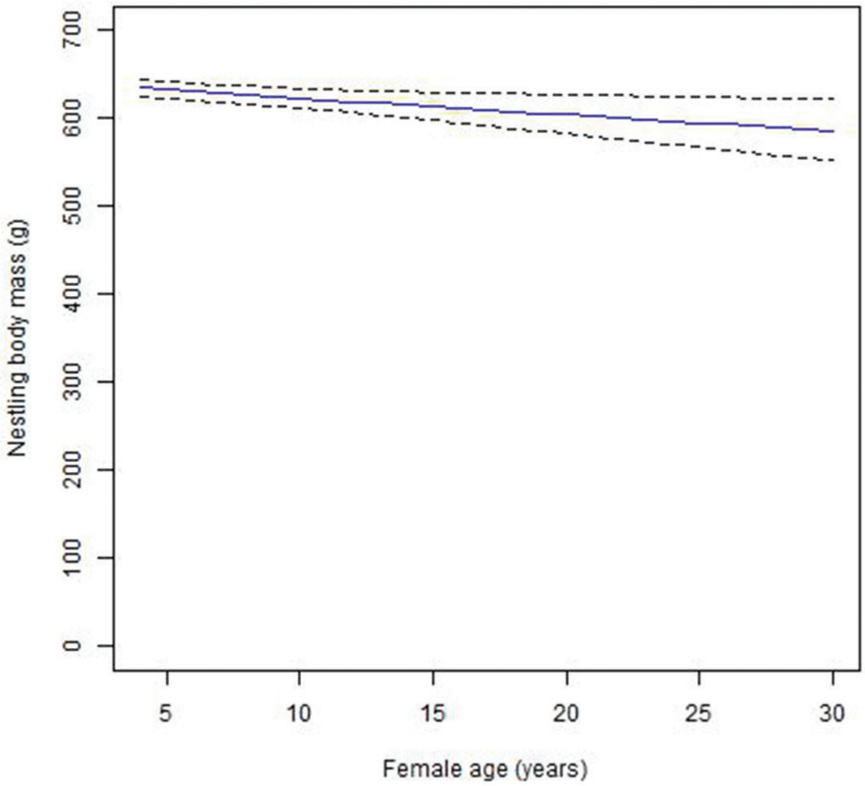

Figure 9. Predicted body mass of nestlings aged 55 days as a function of female age, derived from a GAMM fitted to all observations of nestlings of unknown age females. The dashed lines represent the 95% confidence levels.

Table 2: The change in the week females laid their first egg the following breeding season. Calculations are based on timing of egg-laying by individuals in relation to the start of the breeding season as week 1 (see text for detail).

Change in week egg laid next season	Known age females	Unknown age females
10	0	1
9	0	0
8	0	0
7	0	1
6	1	4
5	0	4
4	1	7
3	0	13
2	1	10
1	3	28
0	1	24
-1	2	22
-2	1	8
-3	1	14
-4	3	13
-5	0	5
-6	1	0
-7	0	3
-8	0	0
-9	0	1
-10	0	1
-11	0	1
-12	0	1
Total	**15**	**161**

commenced (range weeks 1 – 8) that season compared with the 4th week for known age females 7 to 27 years old ($n = 15$) (weeks 2 – 9); this difference was significant (Mann-Whitney U Test $p < 0.01$).

The dates of the first egg laid by 99 females of unknown age were also extrapolated. The median date of the start of egg-laying for unknown age females at least 10 to 19 years old ($n = 25$) was the 4th week (weeks 1 – 8) compared with the 7th week for unknown age females at least 20 – 30 years old) ($n = 10$) (weeks 2 – 14); this difference was significant (Mann-Whitney U Test $p < 0.01$).

Discussion

There have been many studies of wild birds that have shown that the age of breeding individuals (usually females) is closely related to reproductive output, with older individuals arriving earlier in the breeding areas, having larger clutch sizes and producing more nestlings than younger birds (reviews in Lack 1966; Forslund and Pärt 1995; Fowler 1995). In long-lived species of bird that form long-lasting pair bonds, and have distinct breeding and non-breeding seasons, there are often four phases in their reproductive life (Fowler 1995). The first phase is the juvenile or sub-adult phase during which no breeding is attempted, the second is the onset of breeding when breeding success (or reproductive output) is initially lower than that of older individuals (Espie *et al.* 2000; Sánchez-Zapata *et al.* 2000; Vergara *et al.* 2007), the third is more successful breeding with individuals maintaining a high level of fitness, and the final phase is one where breeding success decreases as the individual approaches the end of its reproductive life (Fowler 1995; Ricklefs 2008). In some species this final phase may be short (Ricklefs 2008).

Carnaby's Cockatoo apparently follows this four phase model of reproductive life. The birds form long-lasting pair bonds (Saunders 1982), display breeding site fidelity (Saunders *et al.* 2014b), have distinct breeding and non-breeding seasons (Saunders *et al.* 2013), do not begin to breed until their third or fourth year (Saunders 1982: Dawson *et al.* 2013), and are long-lived (Saunders and Dawson 2009).

There are no data on the timing of the arrival of individuals in the Coomallo Creek breeding area each season, however, the timing of the laying of the first egg each season was extrapolated from nestling ages. Females breeding for the first time chose nesting hollows over a wide range of distances from the hollow from which they fledged (Figure 4). In one case the female nested in the hollow from which it fledged, and the furthest recorded was 8.18 km; from one end of the study area to the other. Once they had bred, most successive nesting attempts were made either in the same hollow (if they had been successful and the hollow was not occupied) or within 1km of their previous nesting hollow. Only 10.4% of all recorded successive nesting attempts were made in hollows more than 1km from the previous hollow, and none were recorded more than 2 km from the previous hollow. It seems that females demonstrated fidelity to the site from which they fledged, and once they have commenced breeding, they demonstrated fidelity to a restricted area of woodland.

Saunders *et al.* (2013, 2014a) showed that over the period 1969-2014 the commencement of egg-laying is strongly correlated with total rainfall in the Austral autumn; the heavier the rainfall, the earlier egg-laying commences, with a variation of eight weeks between the earliest commencement and the latest. At Coomallo Creek females of both known age and unknown age were consistent in the timing of egg-laying in relation to the start of the breeding season. The majority of females laid their first egg within the range of two weeks before or two weeks after they did the previous season. Some individuals laid their egg up to 12 weeks before or 10 weeks after the time they laid the previous season (Table

2). Saunders (1982) noted that females that failed in their first breeding attempt in a season may re-lay and be successful subsequently. In some seasons, the breeding season at Coomallo Creek is long enough for two pairs to be successful in fledging their nestlings in successive uses of the same hollow (Saunders 1982). Those individuals that demonstrated large differences in timing of laying, were most likely as a result of re-lays, with the first attempt in the breeding season not being recorded.

Known age females older than seven tended to lay on average up to three weeks before females 4 to 6 years old. This may be the result of experience, and provides the older females with a wider range of available hollows than those attempting to breed later in the season. This may provide the earlier breeding birds with an advantage should hollows be limiting, something that was almost certainly the case at Coomallo Creek (Saunders *et al.* 2014b). In addition, females of unknown age aged at least 10 to 19 tended to lay in the same period as older known age females. However, females older than at least 20 tended to lay three weeks later, in the same time frame as young, and presumably inexperienced, females of known age.

In Carnaby's Cockatoo there is a period from fledging to commencement of breeding during which juveniles learn to survive in a highly variable landscape. In their first year they remain with their parents, and some may remain with their parents in their second year and return to the breeding area with them (Dawson and Saunders *personal observations*). During this juvenile period the birds form lasting pair bonds (Saunders 1982). Females return to breed in their natal area, in their 3rd or 4th year, often close to the hollow from which they fledged (Saunders *et al.* 2014b). At Coomallo Creek, females breeding in their 3rd and 4th year had known failure rates four times the known failure rate of females in their 5th to 27th years (Table 1). Experience apparently does result in females having a much lower failure rate than young, inexperienced females. The known failure rate of known age females in their 5th to 27th years is similar to the overall failure rate (13.4%) of the 314 breeding attempts recorded by females of unknown age, and to the 14.2% failure rate of the three females of unknown age breeding when they were at least 19 to 30.

At Coomallo Creek the body mass of nestlings produced later in the breeding season was significantly lighter than those produced earlier in the breeding season (Saunders *et al.* 2014a). Although female Carnaby's Cockatoo commonly lays two eggs, on average about eight days apart, incubation commences with the first egg, so the eggs hatch asynchronously (Saunders 1982; Saunders *et al.* 2014c), and the second nestling usually dies within 48 hours of hatching. In up to 5.5% of total breeding attempts at Coomallo Creek both nestlings survive and, in most cases, fledge. When both nestlings fledge, they tend to be to those of older and presumably, more experienced females, and they tend to fledge earlier in the breeding season (Saunders *et al.* 2014c).

Although this study has been conducted for over 47 years, with data available for 28 of those years, the sample size of known age females is relatively small compared with that of unknown age females. While there was a highly significant relationship between nestling age and body mass (Figure 7 and 8), this was not the case with the relationship between female age and the body mass of their nestlings where such a relationship was significant only for the data of nestlings of unknown age females. The model for nestlings of females of unknown age showed a simpler trend in that older females tended to produce lighter nestlings. The average magnitude of the female age effect represents a one per cent decline in nestling body mass for each additional year of the female's age. While small in itself it is a cumulative effect such that over five years we would expect nestlings from an individual female to be 4.5% lighter, and after ten years individual nestlings could be nearly 9% lighter.

Should lighter nestlings be of conservation concern? Saunders (1986) analysed data on body mass (incorrectly termed nestling weight in Saunders' paper) of Carnaby's Cockatoo nestlings from five study areas (including Coomallo Creek) throughout the species' range. He demonstrated that nestlings from three areas had body masses significantly below those from Coomallo Creek. He posited that the populations in those areas were suffering from shortages of food, and that they would likely be extirpated. The population at Manmanning was extirpated by 1977. The species no longer breeds in the other two areas, but there is still a breeding population at Coomallo Creek which is now at a similar size to the population in the late 1960s and early 1970s (Saunders 2014c). There is still a breeding population in the fifth area (Dawson *unpublished data*).

Magrath (1991) revealed a strong and consistent relationship between nestling weight (strictly speaking should be termed body mass) and juvenile survival in the Blackbird *Turdus merula*. He reviewed data on the association between nestling weight and juvenile survival for 18 species of bird (Magrath's Table 5). Eleven species, including Blackbird, Manx Shearwater *Puffinus puffinus*, African Gannet *Sula capensis,* Kittiwake *Risa tridactyla*, Dunnock *Prunella modularis*, Collared Flycatcher *Ficedula albicollis*, Great Tit *Parus major*, Blue Tit *P. caerulus*, House Sparrow *Passer domesticus*, Florida Scrub Jay *Aphelocoma coerulescens* and Crow *Corvus cornix*, showed trends of increasing survival with heavier nestlings. Magrath (1991) used nestling body weight as a measure of nestling quality; the heavier the nestling, the better the quality of the fledgling. He noted "Thus, it might be true that juvenile survival increases with nestling weight in many species but in individual studies it is something to be demonstrated, not assumed." Similarly, Kersten and Brenninkmeijer (1995) found that body weight at fledging of Oystercatchers *Haematopus ostralegus* had a small positive correlation with the probability of the bird's returning to the study area. Naef-Daenzer *et al.*

(2001) also found that survival of juvenile Great Tit and Coal Tit *P. ater* was positively correlated with fledging mass. Nestling body mass does matter, and in Carnaby's Cockatoo may provide indications about the health of breeding populations.

As pointed out by Saunders *et al.* (2014b) the number of known breeding attempts at Coomallo Creek decreased from 88 in 1975 to 32 in 1994, increased to 37 in 2009 and 62 in 2013. In 2014 and 2015 there were 101 breeding attempts. This increase in the number of breeding attempts since 2009 is due to an influx of breeding birds displaced when their breeding sites were destroyed in a wildfire at the end of the 2009 breeding season, the repair of derelict natural hollows and the installation of artificial hollows (Saunders *et al.* 2014b). There was no monitoring of the breeding population between the end of 1996 and the beginning of 2009. In the period when no monitoring took place, farmers in the study area began growing Canola *Brassica* sp. that Carnaby's Cockatoo consume throughout the breeding season and feed to their nestlings. Canola is now a major component of their diet in the breeding season (Dawson and Saunders *personal observations*). The breeding failure rate of the population breeding from 2009 to 2013 was 27.0%, little different from the 30.1% between 1970 and 1977 (Saunders *et al.* 2014b). At present, it is unlikely that food is a limiting factor for the population at Coomallo Creek. Accordingly, the trends in the relationship between female age and nestling body mass are most likely related to the experience of the females; younger, less experienced females tend to nest later and produce lighter nestlings, while older, more experienced females nest earlier and produce heavier nestlings.

It is important to note that the results presented in this paper are based on the study of individually marked females with no information on the influence of males in breeding success. As breeding females are dependent on their partner for food during incubation and the first few weeks of the nestling period, and males also feed the nestling(s), the role of males in fledging young is important. However it is difficult to catch adult males, and time consuming to identify marked males as part of a breeding pair. This is because a marked male has to be recorded copulating with or feeding a marked female or their nestlings/fledglings. There were insufficient data available on breeding pairs where both adults were marked to make any meaningful comments on the effects of male age on breeding success or nestling condition.

It is obvious that female Carnaby's Cockatoo are long-lived in the wild, but how long they survive, and how long they breed is not revealed by this study. One known age female was breeding successfully in her 27th year, and two unknown age females were breeding successfully when they were at least 29 and 30. These females were not seen by us in the breeding seasons of 2015 and 2016. Little is known about longevity of wild birds as few studies have been conducted on marked populations over decades.

Unfortunately most of the information we have on causes of death of Carnaby's Cockatoo come from birds being brought in for rehabilitation. These are mainly due to anthropogenic causes such as collisions with motor vehicles, being shot, being affected by extreme heat and freak hail storms and possible poisoning (Saunders *et al.* 2011b). We know that predation by Wedge-tailed Eagle *Aquila audax* is a natural cause of death (Saunders, 1982), but we have no information on any other natural causes, although research is being undertaken on the Coomallo Creek population to see whether disease is a mortality factor in breeding birds.

Our study on the Coomallo Creek population of Carnaby's Cockatoo has been running for nearly five decades. It has provided much data on the ecology and behaviour of the species, which is useful for developing strategies for their conservation (Department of Environment and Conservation 2012). However it is has not been conducted for long enough to answer the question that we have been asked many times; how long do Carnaby's Cockatoo live? At the time this paper was written, those conducting the field work were 69 and 55 years old, so it may fall to their successors (if any) to answer this important question.

Conservation implications

Apart from this long-term study at Coomallo Creek, little is known about other breeding populations of Carnaby's Cockatoo, apart from the work reported in Saunders (1986). In view of the conservation status of the species, it is important to monitor nestling body mass in other populations of the species, and use the data generated to assess the health of breeding populations throughout the range of the species.

At present the method for assessing nestling quality/health is to use the length of the folded left wing to age the nestling, and then compare the nestling's body mass at that age with a table of body mass and nestling age generated by Saunders *et al.* (2015). Unfortunately this method introduces error associated with the estimate of the age of the nestling. Given the strong relationship between nestling age and body mass (Figure 5), this relationship should be explored, and a table produced for those monitoring breeding populations to assess nestling quality more accurately.

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